calyx is described as small, monophyllous, campanulate, glabrous, parted into 4 straight

FIG. 5.—*Fraxinus sambucifolia* Lam.: Type.

divisions, containing a style "long d'environ cinq lignes" (10 mm). *Fraxinus profunda* is noteworthy for its *relatively* large (about 3 mm long) pistillate calyx. In the photograph furnished by the Paris Museum (Fig. 4) the calyces are not sharply delineated and magnification accentuates the defect; however, they appear to be about 2.5 mm long; that feature, coupled with Lamarck's statement "l'ecore est grisâtre", lends some plausibility to a guess that this specimen might be pumpkin ash. It is hoped that some botanist in or visiting Paris will study this specimen carefully, measure the calyces and also examine the tree (provided it be still standing) to which Lamarck refers. If it is in fact pumpkin ash, the name *F. pubescens* Lam. obviously will have priority over *F. profunda* Bush.

5. FIG. 5, Lamarck's no. 9, "Frene à feuilles de Sureau, *Fraxinus sambucifolia* . . . N." The photograph resembles a somewhat juvenile spray of black ash (*F. nigra* Marsh.); the description also suggests black ash. Sargent (*op. cit.*, p. 37), Sudworth (*op. cit.*, p. 325), Rehder (*op. cit.*, p. 560), and Little (*op. cit.*, p. 192) all remand *F. sambucifolia* to synonymy under *F. nigra*. That appears to be the correct disposition of the name.

ENTOMOLOGY.—*The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing.*[1] GEORGE F. EDMUNDS, JR., University of Utah, and JAY R. TRAVER, University of Massachusetts. (Communicated by Herbert H. Ross.)

The classification of the Ephemeroptera, or of any other group of organisms, should be based upon the phylogeny of the group or, to be more precise, upon a reconstruction of the probable phylogenetic relationship as indicated by all available evidence. This paper presents the results of one phase of an investigation into the problem of establishing a more natural classification of the order Ephemeroptera. The wings of mayflies have

been used as a primary evidence of relationship among extant mayflies and have been the principal evidence available for the classification of fossil forms, many of which are known only as wing prints. To utilize this data to the full it is necessary to be exact in determining the homology of veins and other structures. Thus it was considered necessary to re-examine critically the problem of the wing venation and structure of the mayflies and their fossil allies.

As the study progressed it was realized that there was a correlation between wing structures and the flight pattern of the mayflies studied. This led to an extensive study of the mechanics of flight of the Ephemeroptera. As the Ephemeroptera are

apparently the most primitive of all winged insects, it was subsequently necessary to enter into some of the basic problems concerning the origin and evolution of the insect wing.

STRUCTURE AND MECHANICS OF THE MAYFLY WING

The wing[2] of a mayfly (Fig. 1) is somewhat triangular in outline and has a regular series of corrugations or fluting, which gives it a fanlike form. Each longitudinal vein follows along the crest of a ridge or the bottom of a furrow. Veins that follow ridges are called convex (indicated by a + sign in the figures); those that follow the bottom of the furrows are called concave (− sign). At the margin of the wing there is a complete alternation of concave and convex veins. These corrugations, much as in a fluted fan, greatly strengthen the wing and make it quite rigid. The convex veins and their attached crossveins and membranes act as braces to keep the wing rigid on the downstroke, and the concave veins and their attached crossveins and membranes act as braces to maintain rigidity on the upstroke.[3] The anterior margin of the wing is further strengthened by the close grouping of the costa, subcosta, and radius 1, which are held together at the base by the costal brace. This brace is attached to the convex costa and radius, while the concave subcosta lies between and below and is held firmly in place by the floor of a cup-shaped depression (Fig. 2).

As a result of the above-mentioned structure, the mayfly wing would seem to be rather rigid. This is not entirely so, however, for some of the main longitudinal concave veins, namely Sc, R_{2+3}, MP_1, and sometimes MP_2, have weakened spots called bullae (Fig. 3). In *Siphlonurus* and most of the mayflies, the last vein with a bulla is MP_1, but in some specimens of *Cinygmula* bullae were observed on MP_2. The bullae allow

[2] Reference is always to the forewing, unless otherwise specified.

[3] The physical principles involved in strengthening a plane surface by fluting are widely used in engineering. The fact that corrugated steel is much more rigid than flat sheets depends on the same physical principles as does that of the wing of a mayfly. The fact that the support is primarily a one-way support is readily demonstrated by a common steel rule as used by carpenters, *et al.* When held with the concave surface up, such a rule is so rigid that it supports itself when extended to full 6-foot length, but is so flexible as to roll readily into a small circular case when bent in the opposite direction.

the concave veins to bend, and consequently, during the upstroke, the concave veins fail to support the distal half of the wing. From these facts it can be seen that the corrugations or fluting of the wing and the bending allowed by the bullae serve important flight functions. On the downstroke the wing remains rigid, and the insect gets a maximum amount of lift and propulsion from the stroke (Fig. 4). On the upstroke, however, the distal half of the wing bends downward under the pressure of the opposing air because of the failure of the concave veins, which are weakened by the bullae, to support the wing tip (Fig. 5). The opposing air thus slips away in such a manner as to offer lessened resistance to the upstroke of the wing. The wing tip is the most effective portion of the wing surface because the arc through which the wing travels and the moment of force both become greater as the distance of the wing surface from the point of attachment to the thorax increases.

When the upper and lower surfaces of the wing are separated by soaking in caustic potash it is seen that the costal vein and costal crossveins are equally represented on both surfaces of the wing. All other convex veins are developed almost entirely on the upper surface of the wing, and the concave veins are on the lower surface. Crossveins are found on the upper surface except at the end that attaches to the concave veins where a distinct short section is found on the lower surface (Fig. 6). The veins and crossveins are arranged on the wing surfaces in such a way as to give maximum support during flight. The greatest stress falls on the convex veins and they are noticeably larger than the concave ones. The crossveins are arranged so as to give support on both upstroke and downstroke but the major development of these veins is in that part that attaches to the convex veins.

In the higher winged insects the anterior margin of the wing is quite rigid, and the remainder of the wing membrane is comparatively flexible. These insects fly by means of a sculling action of the wing in which the rigid anterior margin leads the membrane in the direction of the wing stroke. As the wing moves downward, the membrane is inclined upward. This drives the air backward, giving forward thrust, as well as causing a reduced pressure area anteriorly into which the insect is drawn.

In the Ephemeroptera the folding along the line of the bullae (Figs. 1, 5) inhibits sculling
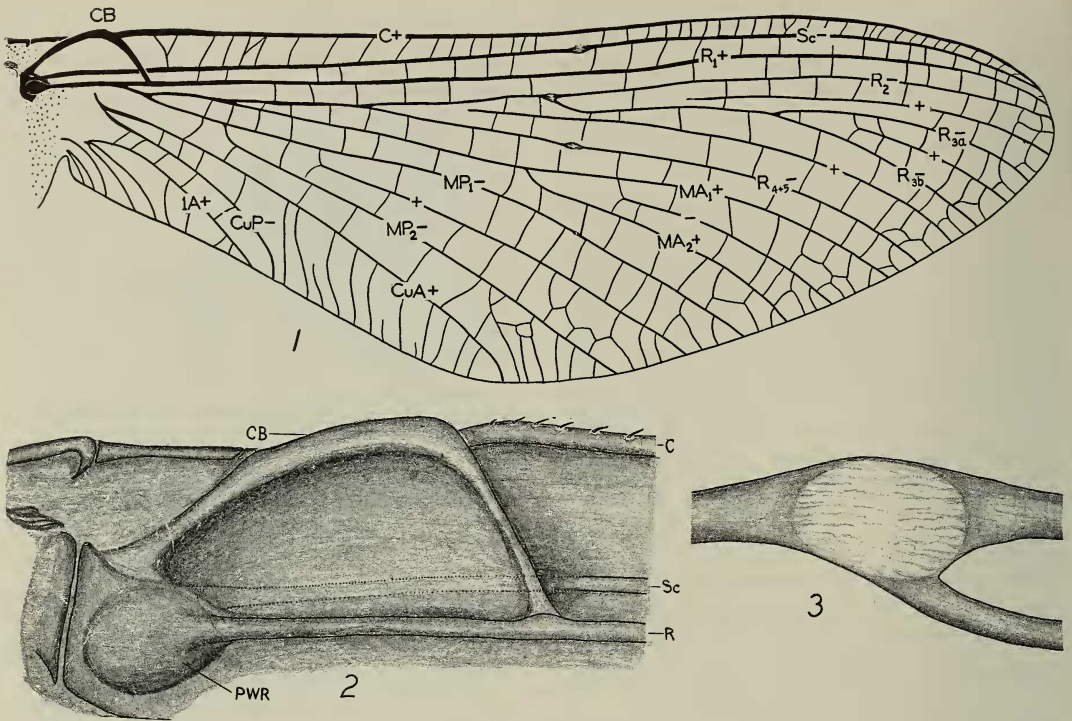
Fig. 1.—Forewing of *Siphlonurus*, showing the bullae and convex ($+$) and concave ($-$) veins.   Fig. 2.—Enlargement of wing base in costal region showing the costal brace (CB) and the pleural wing recess (PWR).   Fig. 3.—Enlargement of bulla at fork of R_2 and R_3.

action to a noticeable degree. It is probable, therefore, that the mayflies obtain their forward thrust primarily from the downstroke, but even then sculling action is not especially effective.

With no problems of obtaining food, the adults of Ephemeroptera have almost every structure adapted for reproductive activity. The wings appear to be no exception to this. The nuptial flight of most mayflies consists of flying upward and then passively coasting or leisurely flying downward. In most species the lines of flight are mainly vertical. The mechanics of flight thus seems to be well adapted for this particular behavior pattern. The corrugation or fluting of the wings also appears to give stability to the downward sailing motion with the wings motionless. Even though the Ephemeroptera have a very primitive wing type, the wing structure is specialized to the degree that it is closely correlated with the behavior of the nuptial flight.

An intensive study was conducted on the wings of *Siphlonurus*, but the other members of the Siphlonuridae, and representatives of the Ametropodidae, Heptageniidae, Baetidae, Leptophlebiidae, Ephemerellidae, Baetiscidae, Ephemeridae, and others, show a similar structure and presumably have similar flight mechanics. The theories of flight functions gained by a study of the wings were tested extensively by means of paper models which performed in the manner which had been already hypothesized on the basis of the study of the structure of the wings. Many direct observations upon the wing motion of the larger mayflies such as *Hexagenia* and *Ephoron* also corroborated these findings to some extent.

An examination of the wings of mayflies belonging to a number of genera indicated some correlation between the degree of development of the bullae and the wing shape. In the genera with long and narrow wings, the bullae are usually well developed on the anterior four, and sometimes five, longitudinal concave veins. Genera possessing shorter and broader wings usually have fewer bullae, feebly developed (probably vestigial) bullae, or both.

THE ARCHETYPE WING

The oldest winged insects are found in the

upper Carboniferous, but it is evident from the great variety of wing types in these fossils that the first winged insects are of greater antiquity. Thus, on the basis of evidence available from the study of fossils and development, entomologists have been forced to speculate on the nature of the first insect wings.

Throughout the winged insects one finds evidence of concave and convex veins. The presence of such a condition led Adolph (1879), and later Lameere (1922), to propose nomenclatorial systems based on the concave or convex positions of the veins.

Forbes (1943) discusses in detail the probable stages in the development of the first wings in insects. He points out the probability that the original wing was a thick process, and he believes that the areas between the veins thinned out and the veins became the main strength of the wings. The present study of the mechanics of the wings of Ephemeroptera has led the writers to believe that the thinning of the wings and the origin of fluting in the wings were simultaneous. As the wings thinned out they needed support, and it is doubtful if the veins themselves could have provided the necessary rigidity. The combination of veins and fluting certainly could have provided better support than the veins alone. That the fluted surface would have provided greater rigidity than a flat surface is easily demonstrated by comparing the rigidity of a flat piece of paper to one that has been fluted by folding. The importance of the veins in establishing this rigidity is pointed out by the fact, as has been mentioned above, that the wing tip loses its support because of the desclerotized areas or bullae on a few principal longitudinal veins.

The actual origin of fluting of the wings is lost in antiquity, but some ideas concerning it have been offered. Needham (1935a) would attribute its origin to the gathering together of the basal connections of the veins as the base of the wing narrowed. Forbes (1943: 393) explains it by the articulation and muscle attachment of a few principal veins to the thorax.

However, once fluting actually started, from whatever cause, it would increase the rigidity of the wing. Once a wing membrane was made more rigid by the fluting, it would have been possible for the wing membrane to become thinner without deleterious effect on the flight powers of the insect.

On the basis of a study of the wings of all groups of insects, living and fossil, Comstock and Needham (1898), arrived at a concept of the hypothetical archetype wing venation (see Comstock 1918: 19). After Lameere (1922) pointed out that the media was composed of two elements, an anterior convex and a posterior concave portion, Bradley (1931) presented a modified hypothetical archetype which included MA. This archetype was modified by Snodgrass (1935: 216) to include the two branches to the anterior division of the cubitus, which had been pointed out earlier by Tillyard (1919). The drawing from Snodgrass has been copied herein (Fig. 7),[4] but the branches of the cubitus have been relabeled to conform to the venational terminology of this paper and signs have been added to indicate the concave or convex positions of the veins.

We herewith propose the hypothesis that the first winged insects possessed a wing that was completely fluted, i.e., had a complete alternation of concave and convex veins at the margin of the wing. Therefore, a modified archetype venation is herein offered (Fig. 8) which includes the intercalary veins necessary for a completely fluted wing. Of necessity, such an archetype venation must include the so-called intercalary veins that are typical of many fossil forms and of some modern orders, principally the Ephemeroptera. Comstock (1918) refers to intercalary veins as veins which arose without a basal attachment, and cites the ephemerid wing as an example. The fossil record clearly demonstrates, however, that the intercalaries of the mayflies were originally attached veins, and that detachment at the base has been a subsequent specialization. A number of the features of the archetype venation are highly questionable because of their great variability in primitive groups. There is reason to believe that subcosta was originally an unbranched vein and that the so-called Sc_1 is merely a realigned crossvein while Sc_2 is the true Sc. It is uncertain as to whether MP should still be considered to be four-branched or if it should be only a 2-branched vein. In what we consider to be the most primitive type of wing as seen in the Syntonopteridae it is only 2-branched, but even the Syntonopteridae have wings that have undergone considerable evolution. Those Palaeodictyoptera that have more than two branches to MP appear to have more specialized wings than do the Syntonopteri-

[4] From *Principles of insect morphology*, by R. E. Snodgrass, courtesy McGraw-Hill Book Co., Inc.

dae. It is, of course, possible that such a wing as illustrated in Fig. 8 could have been the precursor of the Syntonopteridae and those Palaeodictyoptera with more than two branches to MP. The evidence is not sufficient in our estimation to necessitate a relabeling of the branches of MP in the ephemeropteran wing to indicate the possible 4-branched condition in the ancestral stock.

In the foregoing discussion it has been pointed out that fluting actually is a severe detriment to the sculling action of flight. There seems to be little doubt that the sculling type of flight is superior to that of the mayfly type. It is our belief *that fluting of the wing surface was important to the first winged insects for the purpose of strengthening the wing surface and was a necessary requisite before the wing could thin out and form an effective surface for flight. Yet once the wing became thin, fluting actually is detrimental to sculling flight except in the few veins near the anterior margin where rigidity is still required. The trend in the evolution of insects is, in most cases, toward wings which have a rigid anterior margin with a flexible membrane behind.* This type of wing is well adapted for speed in flight, while the fluted wings are essentially lift-type wings. None of the remarks above are intended in the Lamarckian sense, but are meant only to imply that the mechanical fitness of any variation in the wing is the principal selective force determining the general direction of the evolutionary trend. Simpson (1950) has recently remarked that most major trends in evolution are adaptive, and it would appear that this is certainly true in the case of wing structure and venation of insects.

It may well be that the mayflies have maintained functional fluting only because of their unique vertical flight habits, which are dependent upon the bullae.

A number of changes in the venation of the wings of insects seems to bring about flexibility in the wing by destroying functional fluting. A few of these noted during the present study are: (1) the shifting of the position of the longitudinal veins so as to cause them to diverge to the rearward; (2) broadening and shortening of the wing (this often aids process 1, above); (3) migration of concave veins to the vicinity of, and subsequent fusion with, convex veins; (4) elimination or atrophy of intercalary veins; (5) staggering of the path of a vein; (6) desclerotization of veins; and (7) atrophy of crossveins.

The weakening of the wing membrane beyond a certain point is detrimental and those insects which are strong fliers continue to have a well developed system of veins. The problem is most easily explained by the analogous case of fanning air into a fire. If one selects a flat board and waves it much in the fashion of the action of an insect wing, he will find that it is quite ineffective. A small piece of rug which can be held stiff on one margin, however, has a fine sculling action and is much more effective. If for a final test one selects a piece of cloth or paper and holds one edge stiff, the material will prove so pliable as to be of little value in moving air. The wing operates in much the same manner. A wing membrane that is either too rigid or excessively pliant is ineffective; the most effective degree of pliancy is intermediate between the two extremes and undoubtedly varies according to the size and shape of the wing, loading, speed of flight, wing beat frequency, atmospheric pressure, and numerous other factors.

Another evolutionary trend that has been significant in providing an effective sculling surface for insect flight has been the inclusion of the hind wing surface with the forewing by means of coupling devices. Such wing coupling is well known in such insect orders as Lepidoptera and Hymenoptera, but it also occurs in the Ephemeroptera. We have noted such coupling devices in certain Palingeniidae, Polymitarcidae (Campsurinae), Oligoneuriidae, and Siphlonuridae, and a survey of the order may prove wing coupling to be more common than suspected.[5] The nuptial flight pattern of certain Heptageniidae suggests that there is a greater sculling action than the forewing alone would be expected to provide and that the two pairs of wings may be coupled.

Among the smallest insects where the surface area of the insect is large in relation to volume one finds a wide variety of wing types. Many have greatly reduced venation as in the Coccidae, various parasitic Hymenoptera and the tiny Diptera, but even when the wing venation is reduced to an apparent single vein, this is along or near the costal margin of the wing. With reduction of the size of an insect there is an accompanied reduction in the number of wing

[5] Dr. Georges Demoulin has informed us (*in litt.*) that all Palingeniidae, Polymitarcidae (including Campsurinae), Euthyplociidae, and Isonychiidae, which he has examined have the hind wings coupled to the forewings.

veins. Dr. H. H. Ross has informed one of us (personal conversation with G. F. E., Jr. December 1953) that the order in which the wing veins drop out shows a regular parallel deve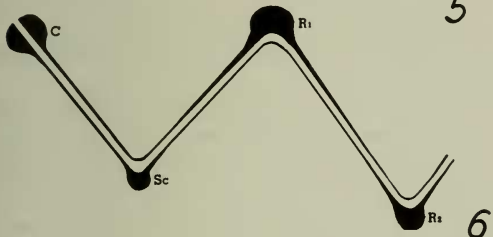lopment in five separate phyletic lines of caddisflies in which reduction of the size of the insect has taken place. Because of the reduced venation among smaller forms, small species are rarely of value in attempting to arrive at a generalized wing venation pattern of any particular taxon.
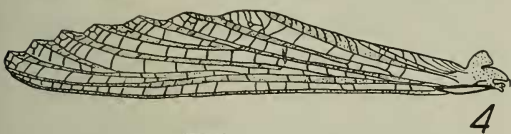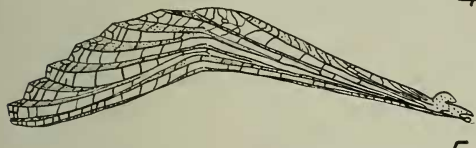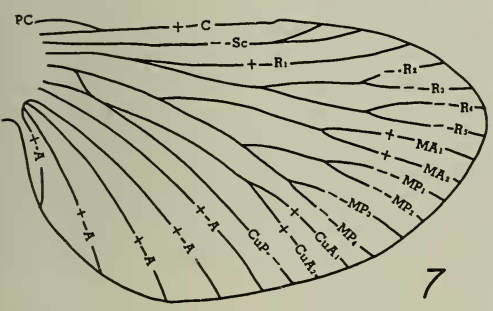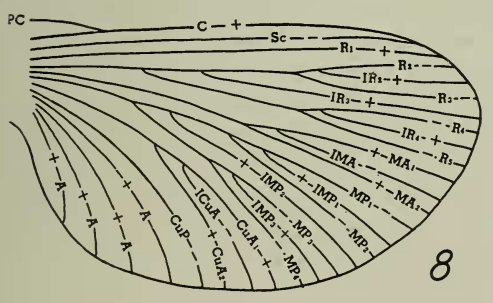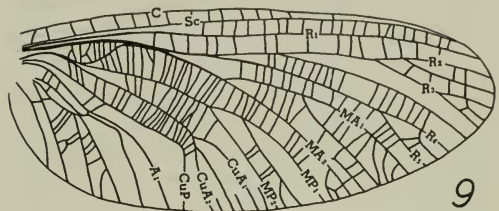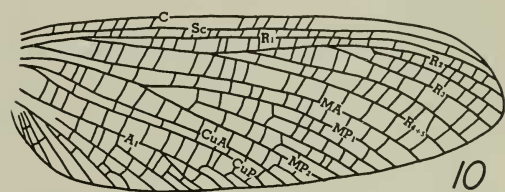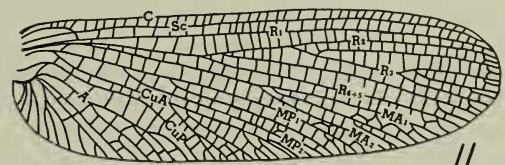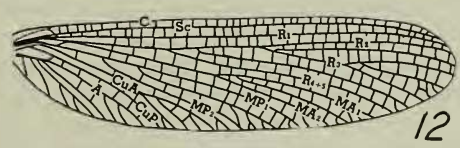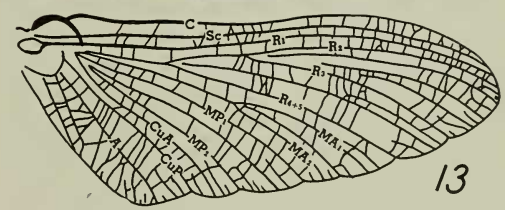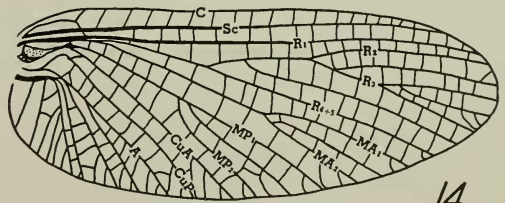
FIG. 4.—Forewing of *Siphlonurus* at midpoint of the downstroke.   FIG. 5.—Forewing of *Siphlonurus* at midpoint of upstroke.   FIG. 6—Cross section of anterior area of forewing of *Siphlonurus*, with ventral and dorsal surface separated.   FIG. 7.—Hypothetical archetype venation (modified from Snodgrass, 1935).   FIG. 8.—Hypothetical archetype venation as proposed herein.   FIG. 9.— Hind wing of *Lithoneura mirifica* Carpenter (modified from Carpenter, 1944).   FIG. 10.—Diagram of hind wing of *Triplosoba pulchella* (Brongniart) (modified from Tillyard, 1932).   FIG. 11.—Hind wing of *Protereisma permianum* Sellards (modified from Tillyard, 1932).   FIG. 12.—Forewing of *Protereisma gracile* Sellards (modified from Tillyard, 1932).   FIG. 13.—Forewing of *Baetisca rogersi* Berner (modified from Berner, 1940).   FIG. 14.—Forewing of *Misthodotes obtusus* (Sellards) (modified from Tillyard, 1932).

Among the smallest insects occur also the forms with fringed wings as in the Thysanoptera, Hymenoptera (i.e., Mymaridae), Coleoptera (Orthoperidae or Corylophidae, and Ptiliidae or Trichopterygidae), Diptera (Nymphomyidae), and some of the small Lepidoptera. Even among these fringed-wing insects the density of the fringe on the wing is directly correlated with size, the larger species having the denser fringe of setae. The independent aquisition of the fringed-wing type by several orders of insects suggests that this wing is particularly suited for flight by smaller insects.

Within the Ephemeroptera representatives of several families seem well on the way toward abandoning functional fluting, and some have completely abandoned fluting and present a well developed sculling-type wing. Members of the families Caenidae and Tricorythidae show a parallel development in that the wings of both are extremely broad and short, the cross venation is greatly reduced, bullae are not evident, and fluting is poorly developed. All of the Caenidae have lost the hind wing and it is much reduced or wanting in the Tricorythidae. The flight of both *Tricorythodes* and *Caenis* differs from the usual type in being rapid with a short vertical undulation.

In the Palingeniidae and Behingiidae the essential fluting has been altered in the radiomedial area by the migration of the concave veins to the vicinity of the convex veins. In the Oligoneuriidae there is a series of genera which show various degrees of fusion of the concave with the convex veins. In *Pseudoligoneuria*, whose wing venation is known only from a study of the nymphal wing pads, the venation apparently approximates the usual type although the concave veins are weak. The genera *Oligoneuriopsis* and *Oligoneuriella* have very weak concave veins which lie next to the convex veins. In *Lachlania* the concave veins lie in folds beneath the convex veins, while in *Homoeoneuria* and *Oligoneuria* the fusion is apparently even more complete. This family (except perhaps *Pseudoligoneuria*) no longer exhibits the conventional type of mayfly flight and has developed a sculling type of flight. The veins have no bullae, crossveins are greatly reduced, and the veins behind R_1 are divergent from the longitudinal axis of the wing. Also the wing membrane remains pliant because these mayflies fail to shed the subimaginal pellicle from the wings—it is shed only from the body, legs, and tails. The flight of *Lachlania* lacks the typical

vertical pattern, and is extremely rapid and powerful. We have observed males of *Lachlania* making progress upwind against a breeze that would drive individuals of most other mayfly genera from the air. Mayflies of this genus have an excellent flying power that clearly demonstrates the superiority of the sculling type of flight for speed and power.

If functional fluting is maintained, as it is in most mayflies, the venational changes, except for modifications in the basal connections or path of a vein, are distinctly limited. Almost all changes in the main venational pattern fall into the categories of either (1) branching of existing veins with the formation of an intercalary vein, or (2) simple fusion of two branches of the same vein with the elimination of the intervening intercalary.

As functional fluting disappears changes in the venation are not as limited, and may include such possibilities as: (1) atrophy of a vein; (2) addition of a vein; and (3) fusion of veins of opposite sign, i.e., a concave and a convex vein. Even when one considers the great number of venational changes that are possible, it seems that many have come about primarily by simple fusion of the branches of a vein. It would cause much less upset in the mechanical action of a wing to reduce a vein by fusion of its branches than it would if the vein were to drop out completely. Students of wing venation should give serious thought to the possibilities of explaining present wing venation by fusion before assuming that a vein is lost.

Except for the veins along the anterior margin of the wing, fluting or alternation of concave and convex veins would seem to be of little use to insects that have a sculling type of flight. Also there is no apparent reason why convex veins should belong to the upper surface and concave veins to the lower surface in such forms. Yet, the fluting of wing veins is found in practically every order of insect and even when fluting is obscure, the separation of the wing surfaces often reveals which veins are concave and which are convex. The logical explanation appears to us to be that the fluted type of wing is the ancestral type and that the convex and concave vein positions are nonfunctional in most modern insects and are to be regarded as vestigial conditions. If this is true, then the concave or convex positions of veins should be valid evidence for establishing vein homologies. The present study, however, points out one possible pitfall

in using this evidence alone. In the wing of *Lachlania* where the concave veins are now in the process of fusing with the convex ones, R_3 has lost its identity by having its distal half under IR_3. Thus, in a fundamentally concave area of the wing, it is evident that the sole surviving vein in the center of the radial sector will be a convex intercalary.

In many groups of insects a careful study of concave and convex vein positions will, when used in conjunction with other evidences, lead to a more clear exposition of wing vein homologies. Positional evidences are the most important single evidence in interpreting vein homologies in the Ephemeroptera; without this evidence determination of the venational homologies of the highly modified wings of the Oligoneuriidae would probably have been impossible. In other groups of insects in which the wings are greatly modified venational positions will probably yield a minimum of evidence. In some insects some of the wing veins are convex at the base and concave distally (or vice versa). In such cases the vein positions may be a result of secondary modifications but in others such evidence may aid in interpreting vein fusions. An example of the latter type is found in the dragonflies, where the concave subcosta has fused with the convex costa beyond the nodus and has imparted a concave nature to the combined costa and subcosta along the leading edge of the wing.

ORIGIN AND EVOLUTION OF THE EPHEMEROPTERA

If the archetype venation proposed herein is accepted, the most primitive known winged types are found in the family Syntonopteridae of the Palaeodictyoptera. The main difference between syntonopterid venation and that of the archetype is that R_3 has formed a triad (although this may have been an archetype feature), and there have been some changes in the basal connections in the hind wing. In the genus *Syntonoptera*, MA is independent of Rs, but in *Lithoneura* (Fig. 9) MA has branched anteriorly near the base to fuse for a short distance with Rs. Carpenter (1938: 450) remarks that "It is very probable that the family Syntonopteridae occupied a position in the Palaeodictyoptera not far from the stock which produced the Plectoptera [= Ephemeroptera]." We would agree with Carpenter although we would note that the wings of the Syntonopteridae have no features which would preclude their inclusion among the

Ephemeroptera.[6] The Palaeodictyoptera are characterized by having two cerci, while the mayflies have two cerci *plus* a median filament (although this is greatly reduced in about half the extant families); the number of caudal filaments of the Syntonopteridae is unknown. The point seems minor, but may be fundamental. If we accept the belief that Machiloid-like Thysanura were ancestral to the winged insects, then it seems likely that the first winged insects would agree with their thysanuran ancestors in having three caudal filaments. We suspect not only that the Syntonopteridae might have had three caudal filaments but that possibly they were true Ephemeroptera. We are also inclined to suspect that further discoveries of fossils of primitive winged insects might lead to the conclusion that the Palaeodictyoptera themselves represent a specialized offshoot from the Ephemeroptera rather than being ancestral to them.

Although the mayflies are generally considered to be the most primitive of winged insects, most workers have considered the fluting and intercalaries of the mayfly wing to represent specializations rather than a primitive condition. Tillyard (1932: 105), however, is inclined to regard the wing venation of mayflies as the most primitive of all insects, both fossil and recent, but, of course, the wings of the fossil genus *Lithoneura* were unknown to him.

Tillyard (op. cit.: 102) seriously questioned, but did not completely reject, the view of Martynov (1923) that the Dictyoneuridae and the genus *Triplosoba* (Protephemeridea) (Fig. 10) were the ancestors of the mayflies. While *Triplosoba* has the general facies of a mayfly, has three caudal filaments, and has retained the complete alternation of concave and convex longitudinal veins, the simple condition of MA[7] and the backward slanting of all the branches of Rs behind R_2 so as to form a somewhat pectinate Rs show specializations toward the sculling type of flight. There are, in our opinion, no members of the modern mayfly fauna that give any indication of having arisen from the Protephemeridea as represented by *Triplosoba*. Tillyard (loc. cit.) suggests that the Prote-

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[6] Our judgment of the phylogenetic position of the Syntonopteridae is based primarily upon the fossils of *Lithoneura* rather than upon the fragment of the wing of *Syntonoptera*.

[7] The original figure of the wings of *Triplosoba* by Brongniart (1893) shows MA arising from R_1 rather than from MP as in the subsequent figures published by Handlirsch (1908) and Tillyard (1932).

phemeridea represent a side branch not in the direct ancestral line of the true Ephemeroptera, and Needham (1935b: 207) and Martynov (1938) have indicated a similar position for this form. As *Triplosoba* has three tails present, the cerci plus a median filament, a condition shared with the true mayflies of the Permian, it would seem likely that if we are correct in assuming a common ancestry for *Triplosoba* and the Syntonopteridae, the latter may, as we have remarked above, prove to have three tails, when and if specimens are found with these structures preserved. The position of the Dictyoneuridae would seem to be even more remote from the ancestral stock of the mayflies.

Tillyard (op. cit.) has discussed at length the possibilities concerning the relationships of the Permain Protereismatidae and Misthodotidae to modern mayflies. While he draws no definite conclusions as to which family gave rise to Recent forms, he states that the evidence favors the Protereismatidae. He seems concerned about his failure to demonstrate the presence of the CuA triad of Protereismatidae (Figs. 11, 12) in extant mayflies. The CuA of the forewing of most Siphlonuridae (Fig. 1) is so similar to the same vein in the hind wings of some species of *Protereisma* (Fig. 11) that it is difficult to understand Tillyard's concern on this point. Indeed, the CuA triad can be detected in most modern genera of mayflies and is very well developed in some Ephemeroidea.

Tillyard noted that the otherwise primitive wing of *Baetisca* (Fig. 13) shows no sign of a triad on CuA. *Baetisca* and its somewhat aberrant relative, *Prosopistoma*, have long been recognized as being markedly distinct from the remainder of the mayflies. The wings of *Baetisca* are so fundamentally similar to those of Permian family Misthodotidae (Fig. 14), which likewise lacked the cubital triad, that it would seem most logical to account for the distinctness of *Baetisca* and *Prosopistoma* by assuming that they originated from the Misthodotidae or some misthodotid-like group. On the basis of their cubital veins all the remaining mayflies probably arose from the Protereismatidae or some protereismatid-like form, although it is possible that the Palingeniopsidae or some related form gave rise to the burrowing mayflies (Ephemeroidea).

VENATIONAL NOMENCLATURE OF THE MAYFLIES

At the present time there is some dispute over the nomenclature and homologies of veins of the mayfly wing. The history of the venational nomenclature of the mayflies has been adequately reviewed in several publications (Tillyard, 1932: Spieth, 1933; and Needham, 1935b) so the treatment here will be limited to a discussion of the identity of the vein variously called MA or R_4 and R_5. In 1923, Tillyard proposed a system of nomenclature based on studies of fossil forms, and adults and nymphal wing pad development of some primitive modern genera. At this time he had not yet seen the paper by Lameere (1922) in which it was recognized for the first time that the media was composed of two parts, an anterior convex and a posterior concave element. In 1926, Tillyard modified his earlier system by recognizing the median anterior vein (MA) of Lameere. He again modified the system slightly in 1932 to make the venational symbols coincide with the Comstock-Needham system.

Needham (1935b) concludes that MA is not represented in the mayfly wing. He therefore proposed a nomenclature which is somewhat similar to Tillyard's (1923), but he made several small, yet significant, changes. Forbes (1943) reviewed the problem again and accepted the Needham nomenclature except that he refers to the Cu_2 of Needham as the plical vein.

At the present time both the Needham system of 1935 and the Tillyard nomenclature of 1932 are in common usage. There is but a single major point of disagreement between the two aforementioned systems, namely: Is the convex vein which lies between the concave radial sector and the concave media part of the radial sector or is it media anterior (MA)?

From the previous discussion it is obvious that the Tillyard system of 1932 has been accepted in this paper. His interpretations appear to be correct and are given support by two new evidences: (1) the discovery and description of the two fossil species of Syntonopteridae, *Lithoneura mirifica* and *L. lameeri*, and clarification of the position of *Syntonoptera* by Carpenter (1938, 1944); and (2) the present work on the mechanics of flight of mayflies.

The wings of the family Syntonopteridae are remarkably primitive and very similar to the archetype venation herein proposed. Radial sector is five-branched as the result of the formation of a triad on R_3. In the genus *Syntonoptera* MA is entirely free from Rs although it does arch toward it basally. In the wing of *Lithoneura mirifica* Carpenter (described from Mazon Creek, Illinois, Upper Carboniferous formation)

MA branches anteriorly, fuses for a short distance with the base of Rs and then continues as a convex vein.

In comparing members of the pre-mayfly family Syntonopteridae with the Permian mayflies of the family Protereismatidae (figs. 11 and 12) only a few differences are evident. In the latter a few veins have different courses, the forks are deeper, and R₄ and R₅ are fused. The main point of interest here is that MA is *still attached to MP basally but arches forward as in Lithoneura* to fuse with Rs for a short distance before continuing on as a convex vein. Tillyard (1932) pointed out the evidence of this fusion in *Protereisma*, but it is much more pronounced in *Lithoneura*.

.The essential difference between the venation of the Permian *Protereisma* and the modern Siphlonuridae is that the basal connection of MA to MP has been lost and MA appears to arise from Rs. Actually, in the Recent genera studied in the present work, the bases of Rs and MA are independent and merely abut against one another.

The fact that the concave or convex positions of the vein serves an important function in flight most certainly would seem to preclude the possibility of complete loss of MA and the substitution in its place of parts of Rs which would apparently have had to change from concave to convex. The function of the wing would, however, be in no way impaired by a shifting of the base of MA so that it is associated with Rs rather than MP. There thus seems to be wholly adequate evidence to show that the vein in question was originally part of media and not a part of the radial sector.

The primary evidence for the belief that the vein in question is part of Rs rather than MA has stemmed from the fact that the vein is supplied by a trachea that arises from Rs. The tracheal connections in the developing mayfly wings vary considerably as has been demonstrated by Morgan (1912) and Tillyard (1923), yet the adult wing venation illustrates considerable conservatism. The relative stability of the venation has been imposed by the mechanical needs of the wing, each variation that interfered with the mechanics of flight being eliminated. While the tracheation of the mayfly wing apparently has played an important part in the phylogenetic development of venation, it most certainly does not have enough stability in nymphal mayflies to justify its use in maintaining a venational nomenclature contrary to the evidence from the

fossil record. As Needham (1951) has so aptly pointed out, tracheal evidences are valuable only when used judiciously and with caution. It is possible that the small callus or sclerotized plate in the developing nymphal wing pad of Ephemeroptera may have played a role in uniting MA to the base of Rs, but this reasoning apparently would not apply to the other insect groups where MA has fused with Rs.

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HERPETOLOGY.—*Description of a new frog of the genus* Eleutherodactylus *from Jamaica, B.W.I.* W. GARDNER LYNN,[1] Catholic University of America.

In 1943 Lynn and Dent, in discussing the distribution of the Jamaican frog *Eleutherodactylus cundalli* Dunn, presented a new locality record as follows: "The present collections . . . provide the first record of its occurrence on the south coast. It is the only frog occurring on the hot dry limestones of Portland Ridge. Here it was found in deep caves, presumably the only places where there is sufficient moisture to enable it to survive. The cave specimens are very light gray in color, quite large in size and have a very tender skin that usually tears when the animals are captured."

This record was based on eight specimens taken in two different caves on Portland Ridge on August 19, 1941. Since that time C. B. Lewis, of the Institute of Jamaica, has collected six more specimens on various trips to the region, and the present author, during a year spent in Jamaica (July 1952–September 1953) took 19 specimens in the course of seven visits to the caves. Study of this new material shows that the cave specimens represent a species which, though clearly related to *E. cundalli*, is quite distinct. Portland Ridge is a hilly limestone peninsula projecting into the sea from the south coast of Jamaica, connected with the main body of the island by a marshy plain. As Grant (1940) has pointed out it constitutes a sort of "biological island" with a certain degree of endemism in its fauna. It is therefore not surprising that the only *Eleutherodactylus* taken in the area proves to be distinct from other Jamaican forms.

Eleutherodactylus cavernicola, n. sp. (Fig. 1)

Type.—U. S. Nat. Mus. no. 135239, an adult female from Portland Cave, Clarendon Parish, Jamaica, B.W.I., collected June 28, 1953, by W. G. Lynn.

Paratypes.—U. S. Nat. Mus. nos. 117737–117744, collected August 19, 1941, by J. N. Dent and W. G. Lynn; U. S. Nat. Mus. nos. 135240–135257, collected October 24, 1952, to July 28, 1953, by W. G. Lynn; Museum of the